5 *Developmental variation in the facial skeleton of anatomically modern* Homo sapiens

U. STRAND VIÐARSDÓTTIR
University of Durham

P. O'HIGGINS
University of York

Introduction

An in-depth understanding of how our facial skeletal morphology arises during ontogeny is likely to lead to better understanding of the evolutionary, functional, and environmental influences that underpin variation. Thus, without an understanding of comparative postnatal growth we cannot hope to explain fully variation in the adult facial skeletons of modern and fossil hominins. Further, such understanding opens up new possibilities for practical applications such as the forensic classification by geographic subgroup of the faces of infants and juveniles as well as those of adults. In this chapter we will briefly review what is known of geographic variation and postnatal ontogeny in human crania before describing some of the results of our ongoing studies into interpopulation (geographic) differences and their ontogenetic basis. In so doing, we explore the possibility of classifying subadult material in the same way as is presently routinely carried out for adults.

Our recent studies have highlighted a great deal of variation within modern human ontogeny, as well as an early onset of morphologically distinct, population specific morphologies in modern humans (O'Higgins & Strand Viðarsdóttir, 1999; Strand Viðarsdóttir *et al.*, 2002). These differences in ontogeny between modern human groups can sometimes be of equivalent scale to those documented between species of non-human primates (e.g., O'Higgins *et al.*, 2001). This ontogenetic variability needs to be kept in mind when comparing the development of fossil hominin species to that of a single human

Patterns of Growth and Development in the Genus Homo, ed. J. L. Thompson, G. E. Krovitz and A. J. Nelson. Published by Cambridge University Press.

population, or indeed a conglomerate sample of mixed populations, since such comparisons could lead to overgeneralized or, at worst, erroneous conclusions.

In this chapter we will discuss the variability of modern human ontogeny in the context of population-specific differences in the facial skeleton. To illustrate this we provide an example study to illustrate the differences in facial shape and allometry that exist between modern human populations.

Morphological differences in the form of the craniofacial skeleton in adult modern humans: An overview

Many modern human populations show statistically significant differences in craniofacial form. Early quantitative analyses of differences in the craniofacial skeleton were largely focused on the possibilities of racial identification (e.g., Giles & Elliot, 1962). More recently larger-scale studies have used form variations in the skull as an indicator not only of population affinity, but also of interpopulation relationships, in particular in relation to their evolutionary histories and origins (Hanihara, 1992, 1996; Lahr, 1995). Over the last three decades much of the work on modern human craniofacial diversity has been based on large comparative data sets, such as those collected by Howells (1973, 1989, 1995), and more recently the larger, more comprehensive, data set collected and analyzed by Hanihara (1992, 1996). In addition, studies have been carried out on variation within specific geographic regions, and based on specific morphological or dental traits (Hennessy & Stringer, 2002; Hernandez *et al.*, 1997; Howells, 1986; Lahr, 1995; Stringer *et al.*, 1999; Turner, 1992). Many of these analyses have revealed the same general trends in craniofacial variation in modern humans. Overall, adult cranial variation between populations seems to be relatively limited. Relethford (1994), using Howell's data set, found that only ~10% of morphometric variation in the modern human craniofacial skeleton was expressed as interregional variation amongst major geographic regions. Craniometric variation within regions was greater than average within Africa, and smaller than average within Europe (Relethford & Harpending, 1994).

Some documented patterns of craniofacial variation between modern human groups are repeated in different studies. The most notable is the similarity between Australian and African populations in craniofacial form. Thus, Australian populations align more closely with Africans than they do with geographically closer populations, such as the Melanesians (Howells, 1973, 1989). There are two main hypotheses offered to explain the reason behind the Australian–African similarities. The first emphasizes the possibility of convergent evolution (e.g., due to similarities in climate: Guglielmino-Matessi *et al.*, 1977; Howells, 1989), while the second emphasizes the similarities as being the result of shared,

relatively primitive features, retained from the first appearance of modern humans (e.g., Nei & Roychoudhury, 1993; Stringer *et al.*, 1999). Another example of craniofacial similarities that may not have been expected from geographic distribution is the similarity between Tierra del Fuegans and North American Eskimo (Hernandez *et al.*, 1997). However, since both these populations are cold adapted, this similarity may reflect morphological adaptation to cold climates. Both populations have also been reported to use teeth as tools. Thus a large part of their morphological similarities, in particular increased cranial robustness and craniofacial width, could be due to shared adaptations to masticatory stress (see Lahr, 1995).

All in all, there is little evidence in any study of craniofacial form for a straightforward link between geographical distribution and morphological diversity. Thus, if geographical distribution is a good reflection of the diversification and evolution of modern human subgroups, it seems that while human craniofacial form may be population specific it is not a reliable indicator of evolutionary history. The exception to this is Froment's (1992) study based on 536 modern human groups. He found that the scores of the groups on the two major axes of variation indicated correspondence between the major morphological affinities within the sample and a map of the Old World. His finding indicated an increase in facial breadth going from west to east through the Old World and a decrease in nasal breadth from south to north. However, a close scrutiny of Froment's (1992) results reveals the position of the Africans on the Old World map to be midway between the African and Australian continents, reflecting their close morphological similarity, and not at all a good fit to geography.

Thus, morphological diversity need not necessarily mirror geographical diversity. In contrast, patterns of molecular variation accord to a much greater degree with geography than does morphological diversity (Batzer *et al.*, 1994; Cann *et al.*, 1987; Cavalli-Sforza *et al.*, 1994; Nei & Roychoudhury, 1993). Therefore if geographical dispersal reflects evolutionary history, molecular data appear to be a better indicator of this dispersal than does cranial morphology.

This pattern is likely because the translation of genetic variation into phenotypic variation involves multiple, interacting, and complex ontogenetic mechanisms. Thus, during ontogeny genetic information is translated into the phenotype through the processes of development (changes in shape with age), growth (changes in size with age), and allometry (changes in shape with size). These are subject to genetically and epigenetically mediated environmental influences (such as the climatic similarities between Africa and Australia), and to epigenetic interactions between developing tissues (Scheuer & Black, 2000). In consequence, the correspondence between genetic and phenetic variation is not direct, with phenetic variation reflecting both genetic and epigenetic influences on growth.

General principles of growth in the craniofacial skeleton

Although variation in the form of the adult craniofacial skeleton has been extensively studied little is known about the underlying ontogenetic basis of this variation in morphology. When do differences in form develop, and what are the processes involved?

The facial skeleton is made up of numerous independent bones, each of which grows and develops under the influence of various specific and systemic factors. In addition many of the individual bones can be divided into subunits such as the maxillary alveolus, or the orbital part of the maxilla, which grow to some degree independently from each other. Despite this, the facial skeleton has to remain a functional whole throughout the course of development. This is achieved through constant remodeling of individual bones in order to adapt to changes in size and/or shape of other bones.

Although some workers (e.g., Nur & Hasson, 1984) have claimed that there is a predetermined genetic blueprint for craniofacial shape, most would agree that a combination of genetic and epigenetic influences is responsible for adult facial morphology (Hunt, 1998; Lieberman, 1996). Several ways in which these influences could interact have been postulated (e.g., Sperber, 1989). It could be argued that, being insulated from the world to some degree, the prenatal form of the craniofacial skeleton is largely genetically determined and that it is only after birth that epigenetic influences have major impact. However, the human fetus is not suspended in a mechanically inert medium, but is subject to the forces operating within the womb. It is also capable of frequent and strong movements, the force of which may subject the skeleton to considerable stress. It is therefore likely that prenatally the skeleton adapts to epigenetic influences.

The regulation of growth of the cranium is frequently described in terms of functional matrices that regulate bone modeling and remodeling. The theory of functional matrices was first postulated by Moss (1964, 1968; Moss & Saletijn, 1969a, 1969b). In its simplest form the theory postulates that although the sizes, shapes, and positions of skeletal tissues in the craniofacial skeleton are genetically influenced at the initiation of ossification, any further genetic control acts not directly on the bone itself, but on its associated functional matrices. The functional matrix can be any set of tissues or spaces that guide the size, shape, and position of the supporting skeletal tissue (Ranly, 1980). In the case of the facial skeleton these would include the brain, teeth, eyeballs and muscles, the nasal and oral cavities, and the associated respiratory tract. The theory of functional matrices does not allow for direct genetic control of bone formation at facial or cranial sutures. However clinical evidence does suggest that both sutures and cartilage can regulate their own activity to some extent, e.g., in cases of premature fusion of cranial sutures (Burrows *et al.*, 1999; Ranly, 1980;

Van Limborg, 1970; Wong *et al.*, 1991). Thus, the functional matrix theory can be used to explain many aspects of genetic and biomechanical control of growth and development of the craniofacial skeleton, although its limits and restrictions need to be studied in greater detail (Moss, 1997a, 1997b, 1997c, 1997d).

During growth a large amount of bone deposition takes place at the sutural margins of the craniofacial skeleton. This is said to be because the displacement of bone due to the expansion of the functional matrices causes tension, which stimulates the deposition of new bone (McLachlan, 1994). As the growth of the functional matrices influences the form of their associated skeletal units, the bone is constantly modeled and remodeled through the processes of bone formation and resorption, the ultimate goal of which is to maintain the mineralized bone matrix and the lifelong mechanical integrity of the skeleton (Canalis, 1993; Lanyon, 1993). Some workers choose to make a distinction between modeling and remodeling (Bromage, 1986). Bone modeling is associated with the growth of bones in childhood, changing the form of the growing bone to adapt to changes in size and shape of related elements. Unlike remodeling, it is a continuous process and covers a large surface (Eriksen *et al.*, 1993). Remodeling, on the other hand, is cyclical and usually covers a small area, in response to either unusual intermittent strains on load-bearing bones (Fehling *et al.*, 1995; Heinonen *et al.*, 1995; Lanyon & Rubin, 1984), or the body's need to maintain steady levels of serum calcium (Lanyon, 1993; Parfitt *et al.*, 1983). In the context of craniofacial growth, periosteal remodeling maintains the shape and proportion of bones as well as adjusting them to changes in the shape and location of adjoining elements so that the skull remains a functional whole (for a relatively recent summary of modeling and remodeling see Martin *et al.*, 1998).

Comparative growth of the hard tissues – geometric morphometrics

Much of our recent work has focused on the ways in which ontogenetic processes bring about differences in facial form (e.g., O'Higgins & Strand Viðarsdóttir, 1999; Strand Viðarsdóttir & O'Higgins, 2001; Strand Viðarsdóttir *et al.*, 2002). Recent advances in morphometrics have allowed us to more readily to compare ontogenetic changes in facial shape, without the confounding influence of size (O'Higgins, 2000; Rohlf, 1998; Strand Viðarsdóttir *et al.*, 2002). The methods we employ are those of geometric morphometrics and, in particular, approaches based on the shape space of Kendall (1984). These methods allow us to partition size from shape, while preserving full three-dimensional information on the geometry of the objects under study at all stages of analysis (Dryden & Mardia, 1998). Consequently, the ontogenetic shape changes of a

wide range of organisms have now been studied using these techniques (e.g., Collard & O'Higgins, 2001; Djorovic & Kalezic, 2000; Fink & Zelditch, 1995; Monteiro *et al.*, 1997; O'Higgins *et al.*, 2001; Reilly, 1990; Strand Viðarsdóttir & O'Higgins, 2001).

The partitioning of size from shape is particularly relevant in the investigation of allometry and ontogenetic scaling. Thus, many studies have indicated that, in general, where sexual dimorphism exists in the primate face, it arises principally through ontogenetic scaling such that male and female adult morphologies represent different endpoints on a single ontogenetic trajectory, with female adults usually being smaller than males (e.g., Cheverud & Richtsmeier, 1986; Corner & Richtsmeier, 1991, 1992, 1993; Leigh & Cheverud, 1991; Richtsmeier *et al.*, 1993a, 1993b; Shea, 1983, 1986). A similar mechanism may at least contribute to the ontogeny of facial differences amongst modern human subgroups.

Thus, our own work has revealed that intraspecific differences in modern human facial form come about through three closely interrelated aspects of ontogeny, working either singly or in conjunction: (1) an early (possibly prenatal) onset of population specific facial morphologies; (2) a divergence in the ontogenetic shape scaling trajectories of the facial skeleton; and (3) ontogenetic scaling, where populations have different end (adult) points on the same ontogenetic shape scaling trajectory (referred to as "ontogenetic shape trajectory" elsewhere in this chapter for the sake of brevity) (O'Higgins & Strand Viðarsdottir, 1999; Strand Viðarsdóttir & O'Higgins, 2001; Strand Viðarsdóttir *et al.*, 2002). In contrast to earlier studies of primates cited above, it appears that in some human populations sexually dimorphic features develop through a combination of displacement of the ontogenetic shape trajectory and ontogenetic scaling (Strand Viðarsdóttir, 1999). Further, more recent studies by one of us (P O'H) indicate that in many primate species, such as *Cebus apella* and the papionins, sexual dimorphism develops through a late divergence of the growth vector as well as a relative extension of the male ontogenetic shape trajectory (O'Higgins & Collard, 2002; O'Higgins & Jones, 1998; O'Higgins *et al.*, 2001). These findings further elaborate on the role of ontogenetic scaling as expounded by the workers cited above. There has been no in-depth study of non-sexual intraspecific variation in primates other than humans but research on interspecific variation between non-human primate species (O'Higgins & Collard, 1999; O'Higgins *et al.*, 2001) shows the same processes at work (although to different extent) as those which produce interpopulation variation in modern humans.

We present in this chapter a study examining the ontogeny of adult facial morphology in three populations: French/British Caucasians, African Americans, and Arikara Plains Native Americans. It illustrates the influence of early-established form differences, ontogenetic scaling, and divergence of

ontogenetic shape trajectories in generating differences between modern human populations.

Background to the study

In this study we concentrate on the facial skeleton excluding the mandible because facial and neurocranial growth are subject to different influences (see earlier discussion on functional matrices). Thus by focusing on the face alone we simplify our analysis and its subsequent interpretation.

Facial shape differences between Caucasians, African Americans, and Native Americans are probably the best-documented example of variation in human craniofacial form (e.g., Giles & Elliot, 1962; Gill & Rhine, 1990; Snow *et al.*, 1979). For many years, workers in the United States of America have been aware of the necessity of distinguishing between skeletal remains from these three population groups, not only to aid forensic identification, but also to identify the remains of individuals for potential repatriation and reburial. Consequently, a considerable number of forensic identification techniques have been developed specifically to distinguish between individuals from these three groups (Bass, 1986; Brues, 1990; Giles & Elliot, 1962; Rhine, 1990). There is therefore an additional advantage in focusing on the facial skeleton, in that it has previously been shown to be the most diagnostic craniofacial region of these groups in adults (Bass, 1986).

Although the above-mentioned studies have proved relatively successful at distinguishing between adult human remains, there are few techniques available to identify subadult remains. This lack of suitable techniques is mainly due to the confounding influence of the large-scale ontogenetic allometric changes on recognizing potential population-specific morphologies. These problems can potentially be overcome with geometric morphometric techniques, in which size is separated from shape, and allometry (i.e., scaling of shape) can be analyzed independently of other aspects of shape variability if necessary. Additionally, this study will assess the possibility of using geometric morphometric techniques to classify subadult specimens to the correct population group on the basis of facial morphology. In order to assess the differences in ontogenetic processes between the three groups, we will test three null hypotheses. The methods section details how these hypotheses will be tested.

$H_0 1$: There is no difference in the shape of the facial skeleton between the three populations. Testing of the first hypothesis allows us to examine whether there are statistically different population specific facial shapes for each population, irrespective of the age of the individuals.

Table 5.1 *Description of the samples used in the present study*

	African American	Arikara	Caucasian
Number adults[a]	12 (7M; 5F)	10 (5M; 5F)	10 (5M; 5F)
Number subadults	22	49	49
Total	34	59	59
Minimum age (years) subadults[b]	0.75	2.5	0
Maximum age (years) subadults	16	18	19
Collection[c]	CMNH	UTK	NHM, RCS, MH

[a] M, males; F, females.

[b] Biological ages are given in years, and are estimated on the basis of tooth eruption, as in Ubelaker (1989).

[c] NHM, Natural History Museum London; CMNH, Cleveland Museum of Natural History, Ohio; UTK, Department of Anthropology, University of Tennessee, Knoxville; RCS, Royal College of Surgeons, London; MH, Musée de l'Homme, Paris.

$H_0$2: The differences between populations are inadequate to allow subadult individuals of unknown origin to be correctly assigned to population groups on the basis of facial morphology. The second hypothesis is dependent on the first hypothesis being rejected. The attempt at falsification of the second hypothesis allows us to examine the possibility of correctly identifying subadult individuals to population groups.

$H_0$3: There is no difference between the ontogenetic shape scaling trajectories of the three populations. The attempt at falsification of the third hypothesis examines the evidence for significant divergence in the ontogenetic shape scaling trajectories between groups. It also allows us to consider the extent to which ontogenetic scaling contributes to differences in facial morphology between populations.

Materials

The study includes 152 individuals, ranging from infancy to adulthood, from three geographically distinct populations: Arikara Plains Native Americans (ARIK), African Americans (AFR), and French/British Caucasians (CAUC). The composition and the origins of the populations (i.e., samples) are given in Table 5.1. Great care was taken in specimen selection to avoid bias in sample composition in terms of age and sex, although the availability of material in museum collections did not allow us to gather data from age and sex matched samples. Each subadult individual is assigned a biological/developmental age estimate based on tooth eruption according to the dental standard of Schour & Massler (1941), as adapted for use on non-white populations by Ubelaker

(1989). This estimate of maturation is used simply for the purposes of graphing data and not for subsequent statistical analysis. No attempt has been made to sex the subadult sample. All adults are assigned the arbitrary age of 21 years. In this study, individuals are classified as adults if the third permanent molar has fully erupted and the spheno-occipital synchondrosis has fused. Care was taken to include only young adult specimens, as determined by degree of dental wear, stage of suture closure (Meindl & Lovejoy, 1985), and postcranial parameters (such as pubic symphysis aging and auricular surface aging), where possible (Brooks & Suchey, 1990; Lovejoy *et al.*, 1985).

The facial skeleton of each individual is represented by 26 unilateral homologous landmarks in three dimensions. These were collected using a Polhemus 3-Space Isotrak II electromagnetic digitizer. Unilateral data were used in preference over bilateral data, in order to reduce the number of variables by taking advantage of symmetry (Strand Viðarsdóttir & O'Higgins, 2001). This also allows us to increase the size of the available sample by allowing inclusion of specimens in which one side of the face is damaged. The landmarks are listed in Table 5.2. In order to aid visual interpretation of results, each face is approximated by a three-dimensional surface, obtained by triangulations of landmarks. This surface only approximates the facial skeletal surface and is used solely for visualization purposes; analysis is based only on the three-dimensional coordinates of landmarks.

Methods

The three-dimensional coordinates of landmarks are analyzed using techniques from geometric morphometrics. These techniques preserve complete information about the relative spatial configuration of landmarks throughout an analysis and utilize the properties of Kendall's shape space (see below) (Slice *et al.*, 1996). The shape spaces and associated statistics of these methods are well understood (Dryden & Mardia, 1998) and yield highly visual and readily interpretable results.

The landmarks are registered (superimposed) using generalized Procrustes analysis (GPA) minimizing the sum of squared distances between homologous landmarks by translating, rotating, reflecting, and scaling them to best fit. This registration method does not introduce bias into the distribution of specimens where landmarks vary independently and according to random error (Rohlf, 1999). Scaling is according to centroid size, which is the square root of the sum of squared Euclidean distances from each landmark to the centroid (the mean of landmark coordinates). Centroid size is used in this study as an expression of the overall scale of the landmark configuration, and thus of the face, and to examine allometry and growth. All analyses of shape are carried

Table 5.2 *Landmarks used in the present study*

Number	Landmark definition[a]
1	Bregma
2	Frontomalare orbitale
3	Frontomalare temporale
4	Nasion
5	Glabella
6	Stephanion
7	Frontotemporale
8	Superior rim of the orbit
9	Supraorbital torus
10	Dacryon
11	Zygotemporale superior
12	Zygotemporale inferior
13	Maxillofrontale
14	Zygoorbitale
15	Zygomaxillare
16	Jugale
17	Orbitale
18	Alveolare
19	Nasospinale
20	Alare
21	External alveolus at second incisor
22	External alveolus at canine
23	External alveolus at most posterior tooth
24	Palatine–maxillary suture
25	Infraorbital foramen
26	Staphylion

[a] For further explanation of the anatomical location of individual landmarks, see O'Higgins & Strand Viðarsdóttir (1999).

out on landmark configurations from which centroid size has been partitioned through the scaling parameters outlined above. Information about the centroid size of the individual specimens prior to GPA is retained for the purpose of studying size–shape relationships, i.e., allometry.

The registering of landmark coordinates through GPA results in each specimen being represented as a single point in a non-Euclidean shape space of $km - m - m(\frac{m-1}{2}) - 1$ dimensions, known as Kendall's shape space (Kendall, 1984), where k is equivalent to the number of landmarks, and m denotes the dimensionality of those landmarks. To aid statistical analysis, the points are projected into a linear tangent space (Dryden & Mardia, 1992), and statistical analyses are carried out within that space using standard multivariate methods. This approach is satisfactory when variations are small, i.e., where the data lie

within full Procrustes distance of about $d_f = 0.2$, of the mean as in these data (see O'Higgins, 2000; Dryden & Mardia, 1998).

To explore relative relationships between individual shapes, as in the testing of null hypotheses 1 and 2, principal components analysis (PCA) is used to calculate principal axes of variation in the tangent space. Visualization of shape differences along the principal components (PCs) is obtained by warping the triangulated surface of the mean shape to represent shapes at any position within the plot, using the loadings of original landmark coordinates on these PCs (O'Higgins & Jones, 1998; O'Higgins & Strand Viðarsdóttir, 1999). Cartesian transformation grids, calculated using the method of thin plate splines (Bookstein, 1989), are used to further visualize and interpret shape differences.

To test null hypotheses 1 and 2 we explore the significance of differences between populations. This is achieved by computing Mahalanobis' distances between them, and assessing the significance of these differences with Hotelling's T^2. Further examination of differences between populations is carried out by discriminant analysis. All of these are computed between different populations with PC scores from GPA/PCA using (1) the adults alone, and (2) the combined adults and subadults. Discriminant function analysis can be used to predict group affiliation of unknown specimens. In the context of the present study two methodological issues arise. First, in assessing how well discriminant functions perform, they can be expected to better classify data used to calculate them (calibration data), than data not used in the initial computation (test data). Therefore to assess our discriminant functions, cross-validation was carried out repeatedly, so that each time, one arbitrary individual was excluded from the calculation of the classification function, and then assigned to a group using it. Thus in turn, all the individuals were treated as unknowns. Second, in computing the discriminant function the inclusion of "noisy" data that does not differentiate between groups simply adds to dimensionality often at the cost of discriminatory power. To optimize discrimination in the current analyses we computed functions with increasing numbers of PCs. In doing this we sequentially included lower to higher order PCs until discriminatory power of the functions fell off. This is because higher order PCs tend to "noise," i.e., they contribute to total variance but not to between-group variance. In the case of the adults-only discriminant function, optimal discrimination was achieved with 13 PCs, and in the case of the combined adults and subadult discriminant function, 23 PCs.

In order to investigate commonality of ontogenetic shape scaling trajectories and so to test null hypothesis 3, each population is subjected to a separate GPA and PCA and the relationships between variations in shape (principal component scores) and centroid size are assessed using correlation analysis (Sokal & Rohlf, 1995). In each case only the first principal component showed a large

or significant correlation with centroid size (and incidentally with maturation), and thus well represents the shape scaling or allometric component of the ontogenetic trajectory (the whole of which includes the relationship between shape, size, and age).

The significance of the angle between ontogenetic shape trajectories (represented by PC1 in each of the populations studied following a combined GPA) of pairs of populations is assessed in relation to the distribution of angles between 1000 random resamplings (Good, 1993). These resamplings are such that two groups of the same sample sizes as the true groups are randomly created from the original data and the angle between them recorded. The proportion of times the permuted angle exceeds the true angle approximates the *P*-value for the significance of the true angle.

Since PC1 represents ontogenetic shape changes in all populations studied, "mean adult" and "mean infant" facial shapes are created for each population by warping the mean shape to the extremes of the ontogenetic shape trajectory (for a detailed explanation of this procedure, see O'Higgins, 2000). The resultant coordinates of these estimates of mean shape are subsequently submitted to a separate GPA/PCA to allow ready visualization of differences in ontogenetic shape trajectories between populations.

Where pairs of populations show no significant angle between their ontogenetic shape scaling trajectories (as represented by the PC1s from the analyses of each population) the possible presence of ontogenetic scaling differences between population pairs is assessed by the computation of the mean adult centroid size for each population and relating this to ontogenetic shape trajectory divergence and shape differences between adults. The significance of any difference in facial centroid size is evaluated using Student's *t*-test paying regard to any differences in variance if necessary.

Results

The results are divided into two main sections. The first examines the differences in morphology between populations and relates to the first and second null hypotheses specified earlier. The second compares the actual ontogenetic shape trajectories between populations, and describes the test of the third null hypothesis.

Differences in facial shape irrespective of maturation

Statistical significance of interpopulation differences in *adult* facial shape is examined through computation of Mahalanobis' distances from the specimen

Table 5.3 *Results of the discriminant analyses between adult populations. The upper value in each table element represents the Mahalanobis' distance between the populations, and the lower the corresponding* P-*value from Hotelling's* T^2

Caucasian			
Arikara	6.0582 0.0001		
African American	5.2797 0.0005	4.4101 0.0003	
	Caucasian	Arikara	African American

Table 5.4 *Results of the cross-validation test of the adult populations, based on PCs 1–13. The table lists the percentage of individuals from the known groups (listed in the first column), assigned to each group (listed in the last row) in the cross-validation test. It should be read horizontally for correct interpretation*

Caucasian	88.89	0	11.11
Arikara	0	100	0
African American	10	0	90
	Caucasian	Arikara	African American

scores on PCs 1–13 from a GPA/PCA of the adults alone (Table 5.3). These PCs were found to provide the greatest discrimination between the groups (see methods), and account for >85% of the total variance within the overall sample. A discriminant analysis with cross-validation (Table 5.4) shows that between 89% and 100% (mean 93%) of the adult individuals can be correctly classified to population based on these PCs. There is no significant correlation (see definition of correlation analysis above) between the numbers of individuals in each population and the percentage of correct assignations.

Table 5.5 lists the Mahalanobis' distances between the populations with adult and subadult samples combined based on PCs 1–23 (90% of total variance) that optimize discrimination for these data. Again, all the populations are significantly separated on the basis of facial shape irrespective of the variability in the age of the individuals included in the analysis. This finding is supported by a crossvalidated discriminant analysis (based on PCs 1–23) which correctly assigns 88% to 97% (mean 91.98%) of specimens to the correct group (Table 5.6). The individuals incorrectly assigned spanned all developmental ranges (0.75 years to adult) and were not clustered in particular age groups.

Table 5.5 *Results of the discriminant analyses between full populations (adults and subadults). The upper value in each table element represents the Mahalanobis' distance between the populations, and the lower the corresponding* P*-value from Hotelling's* T^2

Caucasian			
Arikara	3.5093 0.0001		
African American	4.5901 0.0001	4.1586 0.0001	
	Caucasian	Arikara	African American

Table 5.6 *Results of the cross-validation test of the full populations (adults and subadults), based on PCs1–23. The table lists the percentage of individuals from the known groups (listed in the first column), assigned to each group (listed in the last row) in the cross-validation test. It should be read horizontally for correct interpretation*

Caucasian	88.14	8.47	3.39
Arikara	3.39	96.61	0
African American	10	0	91.18
	Caucasian	Arikara	African American

Differences in ontogenetic shape trajectories

In order to investigate the possibility of divergent shape scaling trajectories in the three populations as postulated in the third null hypothesis, the data from all three populations are submitted to joint GPA and separate PCAs are carried out on each population. PC1 is found to correlate significantly with centroid size (and also with biological age) in all populations (Table 5.7). It is the only PC to do so. Therefore, we interpret it to represent ontogenetic allometric shape changes in each population. The relationships between age, size, and shape in the Arikara are plotted in Figure 5.1. Figure 5.1A represents growth (age vs. size), Figure 5.1B, development (shape vs. age), and Figure 5.1C, allometry (shape vs. size). The loadings of shape coordinates on PC1 are presented as visualizations of shape change along this axis with overlain Cartesian transformation grids in Figure 5.2.

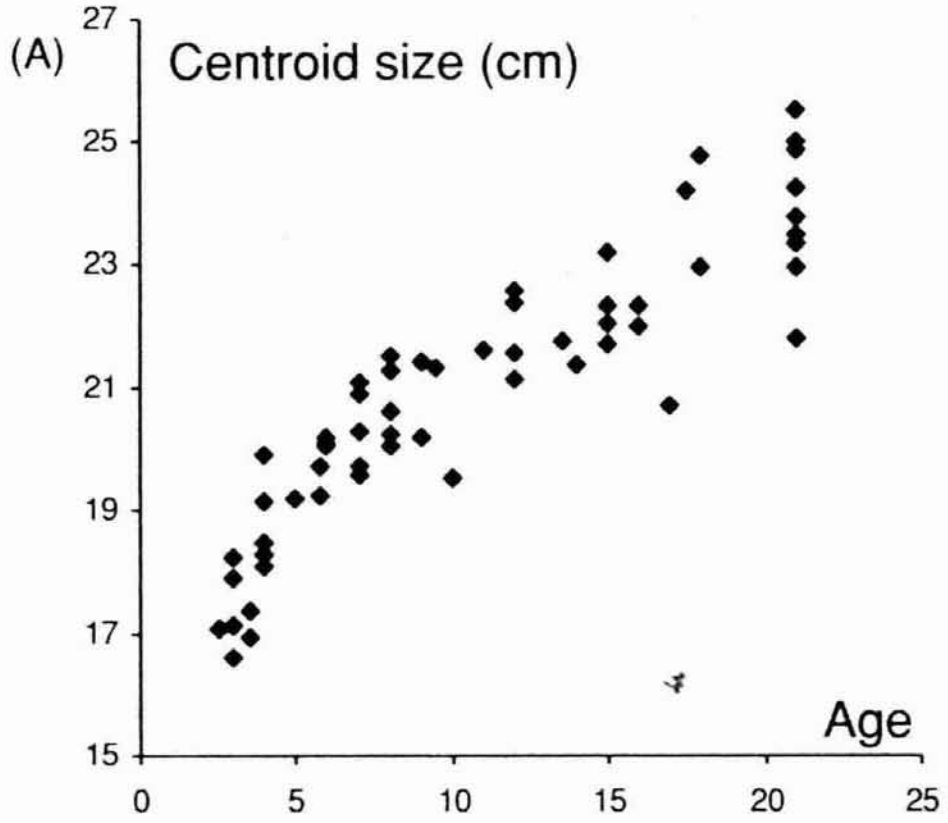
Table 5.7 *Correlations between PC1 and facial centroid size, PC1 and biological age, and facial centroid size and biological age, for each of the samples studied*

	PC1 vs. size	PC1 vs. age	Size vs. age
African American	$r = -0.900$	$r = -0.896$	$r = 0.896$
	$P = 4.18*10^{-13}$	$P = 5.27*10^{-11}$	$P = 7.57*10^{-13}$
Arikara	$r = 0.900$	$r = 0.890$	$r = 0.90$
	$P = 1.39*10^{-21}$	$P = 8.93*10^{-21}$	$P = 2.01*10^{-22}$
Caucasian	$r = -0.930$	$r = -0.901$	$r = 0.842$
	$P = 5.11*10^{-11}$	$P = 1.25*10^{-18}$	$P = 3.56*10^{-14}$

Table 5.8 *Pair-wise comparisons of the angle between PC1s. The upper value denotes the angle, in degrees, between the PC1s of the populations being compared, and the lower the corresponding* P-*value assessed by a permutation test*

African American			
	21.4		
Arikara	$P = 0.0669$		
	23.6	24.1	
Caucasian	$P = 0.0049$	$P < 0.0009$	
	African American	Arikara	Caucasian

Viewed in isolation the relationships between size, PC1, and maturation look similar across all populations (Figures 5.1, 5.3, and 5.4). However, the Cartesian transformation grids reveal individual variations in craniofacial allometry, superimposed on the shared ontogenetic allometric shape changes. Thus the Caucasians show a marked contraction in the supraorbital area with increasing size (Figure 5.5, point 1), not noted in the other populations. This implies that while all populations follow ontogenetic allometric trends with shared features, they also appear to show some distinct aspects of ontogenetic allometry. To assess the possibility of divergence in ontogenetic shape scaling trajectories between populations a pairwise comparison of angles between PC1s is carried out. The results are given in Table 5.8. A permutation test indicates that two out of the three comparisons reveal a statistically significant difference in the direction of the PC1 (ontogenetic shape trajectory) between the two populations compared. Thus, ontogenetic shape changes in the Caucasian sample are



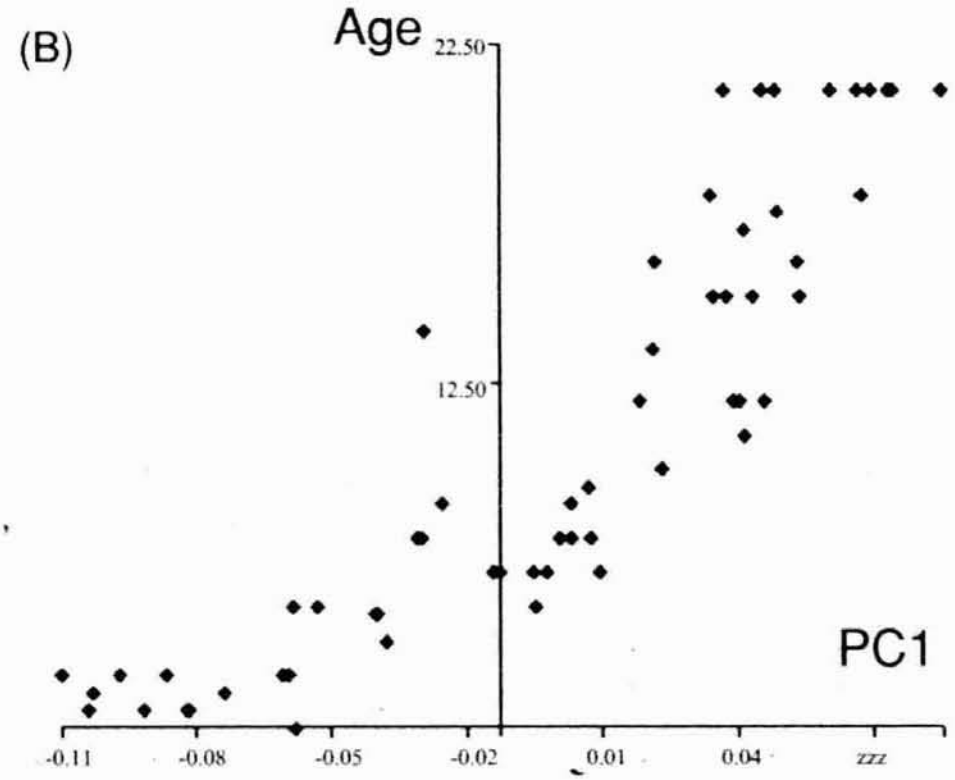


Figure 5.1 Arikara Plains Native Americans: (A) Biological age vs. centroid size; (B) biological age vs. PC1; (C) centroid size vs. PC1.

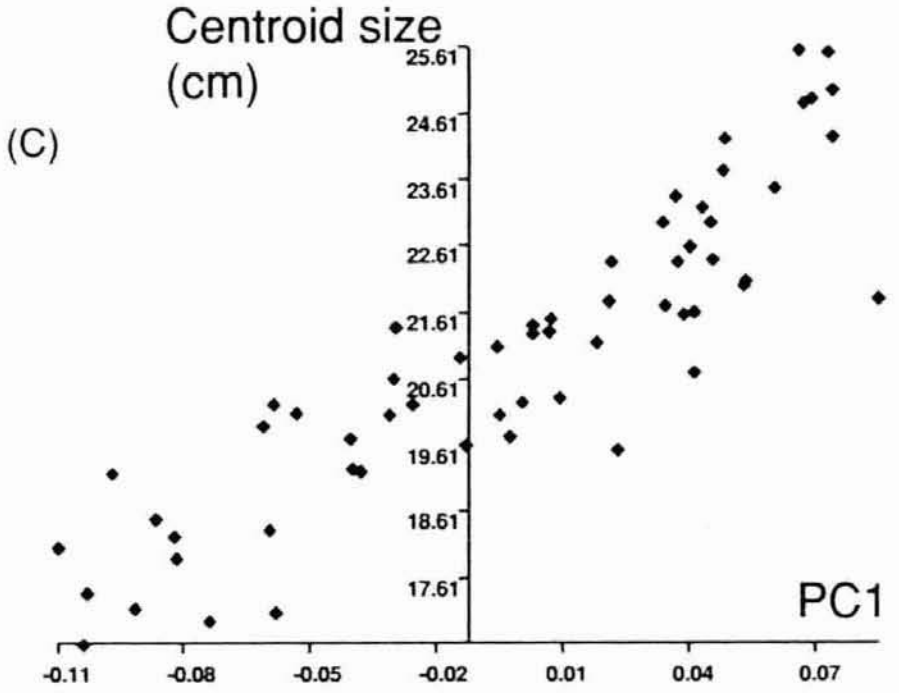


Figure 5.1 (*cont.*).

significantly different from those of both the Arikara and the African American samples. Ontogenetic shape trajectories of the Arikara and African American samples are not significantly different ($P = 0.07$) from one another, although that comparison only just exceeds the 95% significance threshold, thus a slightly larger sample might have given a significant result. These results indicate that at least between the Caucasians and the other two populations (and possibly between all three), differences in adult face shape arise partly through differences in the ontogenetic allometric trajectories, the shape component of which is here represented by PC1. Thus, differences in ontogenetic allometric trajectories actively contribute to differences in adult facial shape.

A comparison of adult facial sizes (Table 5.9) reveals that there are no significant differences in facial centroid size between the adults of the three populations, thus precluding the notion of allometric scaling.

Table 5.9 *Pair-wise Student's* t*-test of the difference in centroid size between adults of the three populations*

Caucasian			
Arikara	$t = 1.941$		
	$P = 0.069$		
African American	$t = 2.23$	$t = 0.077$	
	$P = 0.056$	$P = 0.9400$	
	Caucasian	Arikara	African American

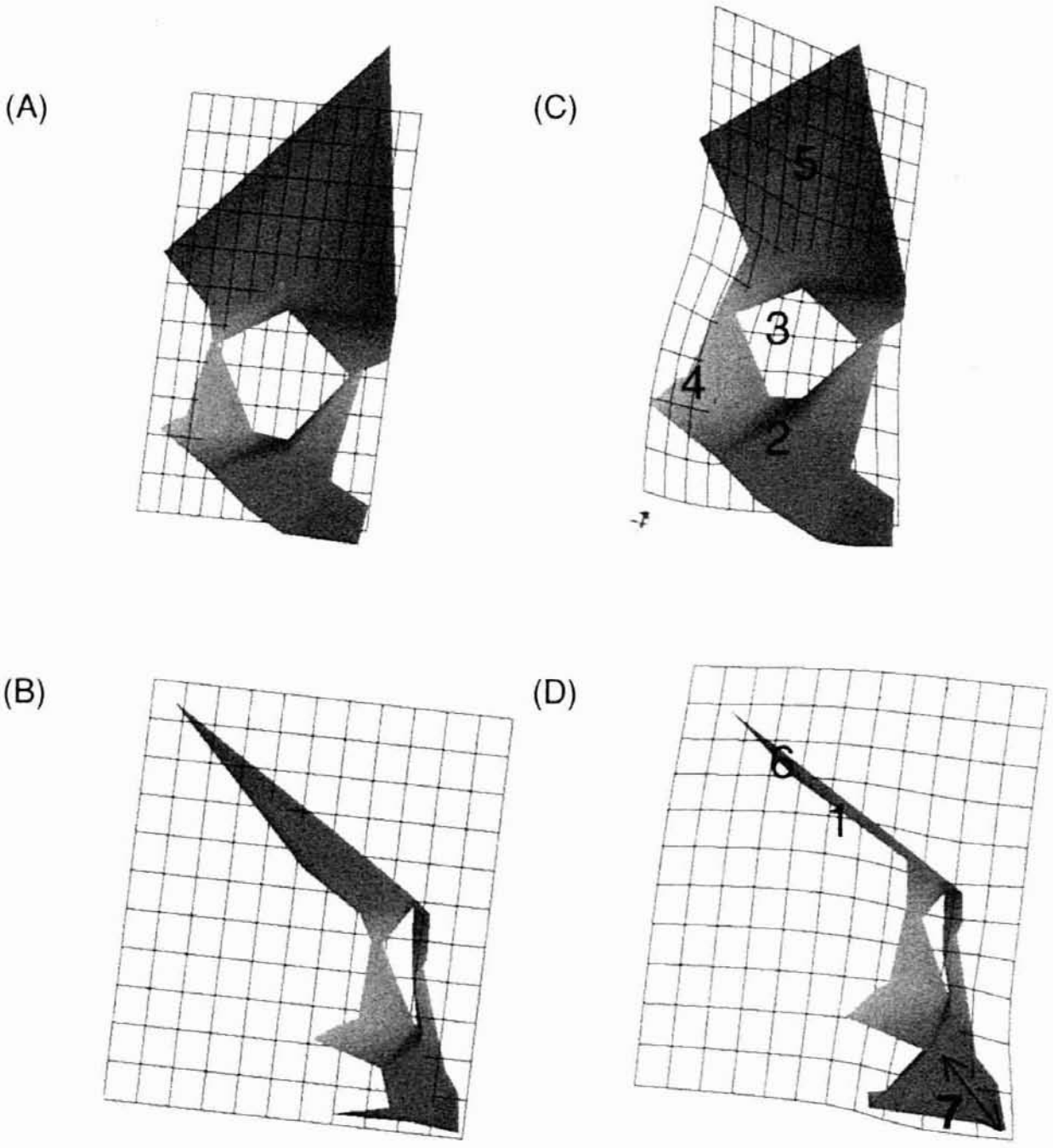


Figure 5.2 Arikara Plains Native Americans: Morphological representations and transformation grids showing the variation in facial shape represented by PC1, from the negative (left, reference: PC1 −0.10) to the positive extremes (right, target; PC1 0.09), frontal (top) and lateral (bottom) views. See text for explanations of numbered labels.

Discussion

The results presented in the previous section have falsified the first and second null hypotheses. Thus, $H_0 1$, that there is no difference in the shape of the facial skeleton between the three populations irrespective of age, is falsified by the discriminant analyses. These indicate that differences in facial shape

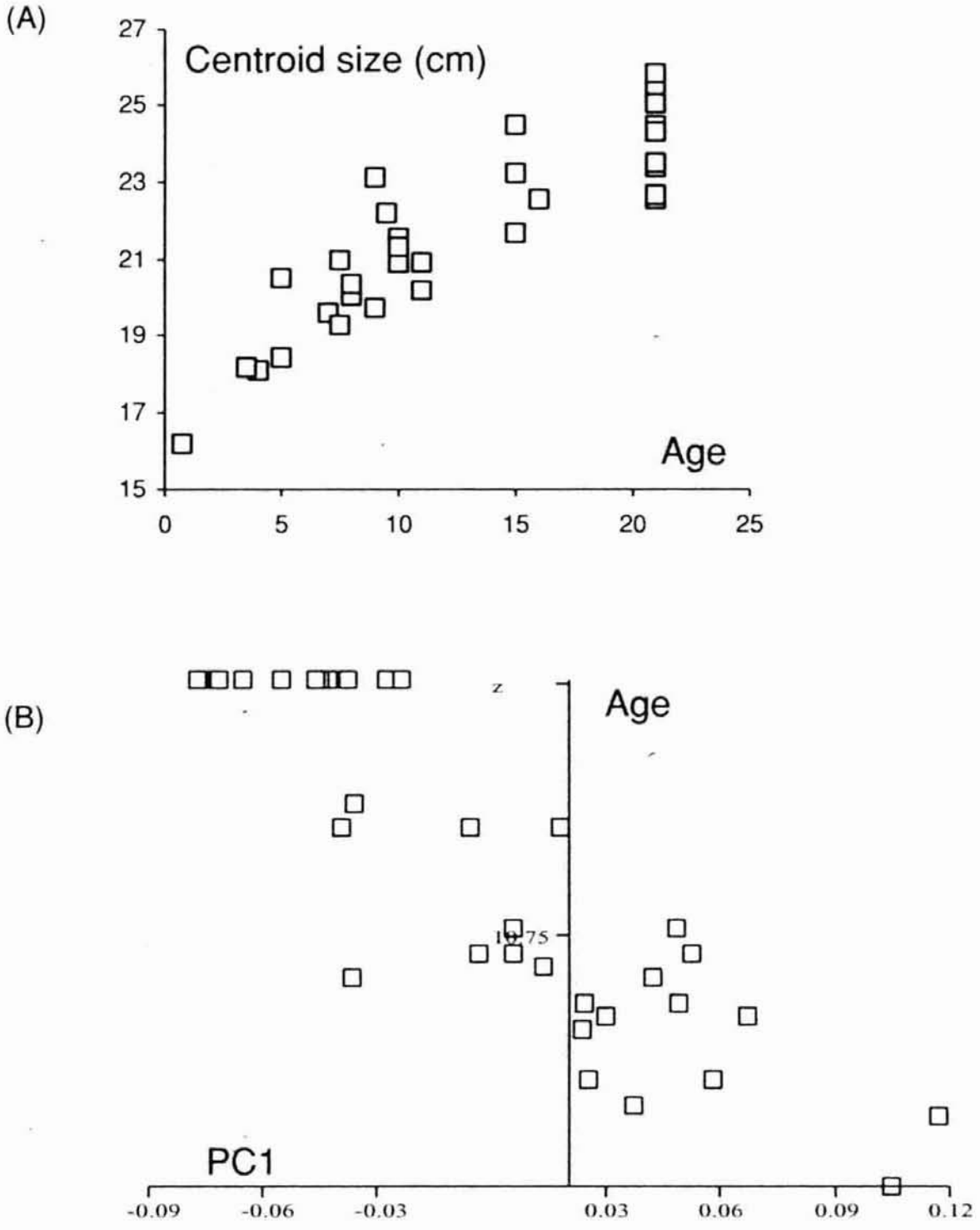


Figure 5.3 African Americans: (A) Biological age vs. centroid size; (B) biological age vs. PC1; (C) centroid size vs. PC1.

between the populations are present even in the smallest/youngest individuals, arising at least in early infancy or even prenatally. These differences are sufficient to allow "unknown" subadults to be correctly assigned to population groups. These findings also falsify $H_0 2$. The significant differences in angles between ontogenetic shape scaling (allometric) vectors falsify the third null hypothesis, $H_0 3$.

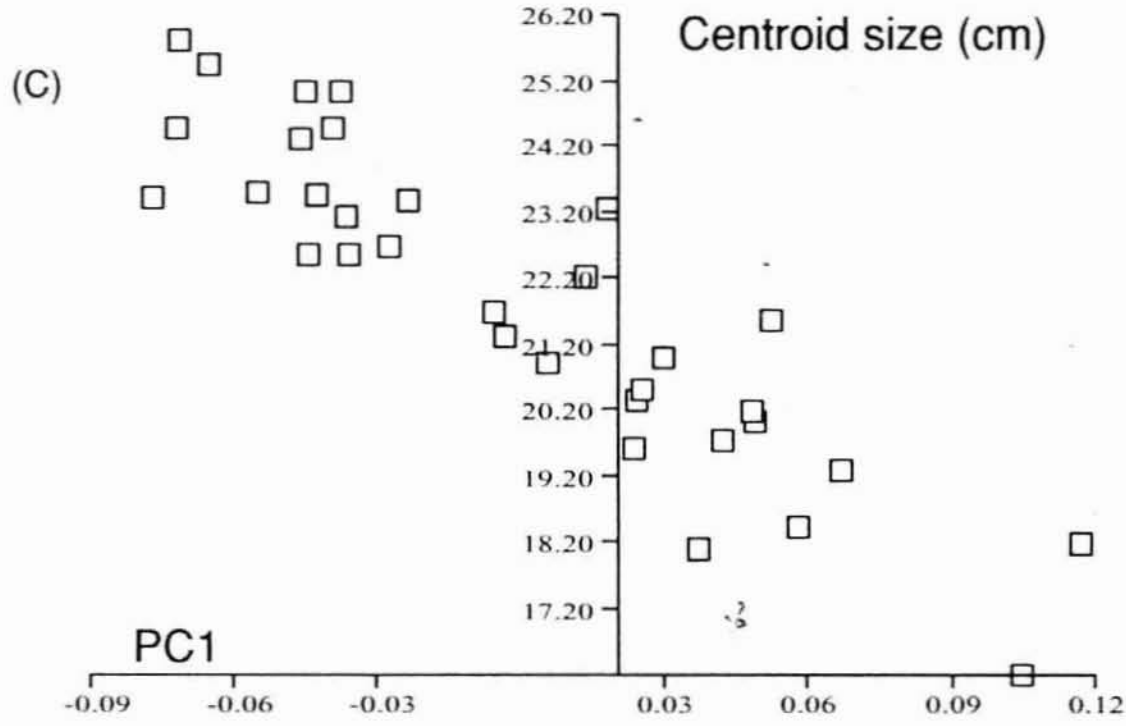


Figure 5.3 (*cont.*).

These findings show that with a sample of three populations we can demonstrate at least two ways by which differences in adult facial shape arise: through an early onset of population specific morphologies, and divergent ontogenetic allometries. Larger-scale studies of a greater number of populations (Strand Viðarsdóttir *et al.*, 2002) have also revealed that for certain population comparisons there is evidence of ontogenetic scaling of non-divergent allometric trajectories.

The analyses of Figures 5.1 and 5.2 examine ontogenetic changes in size and shape in one population, the Arikara. It is interesting to note that in both the plot of growth (Figure 5.1A) and that of development (Figure 5.1B) the scatter of points is curvilinear, indicating that the rates both of shape change and of size increase fall off with increasing maturity. In contrast the plot of allometry (Figure 5.1C) is linear, indicating that the rate (and the anatomical nature) of ontogenetic shape change with increasing size remains constant throughout the range of ontogeny we sample. The plots for the other populations (Figures 5.3 and 5.4) show similar features as do plots for several other primates (e.g., Cobb & O'Higgins, 2002; O'Higgins & Collard, 2002; O'Higgins *et al.*, 2001), indicating that decrease in the rate of shape and size change is common.

This constant increase of size with shape throughout ontogeny in turn points to incremental increases in the size and shape of the functional matrices controlling this allometry, which in themselves are constant in effect across the entire ontogenetic period. Thus, major morphological changes in the facial skeleton during ontogeny are very closely linked to facial size, irrespective of growth

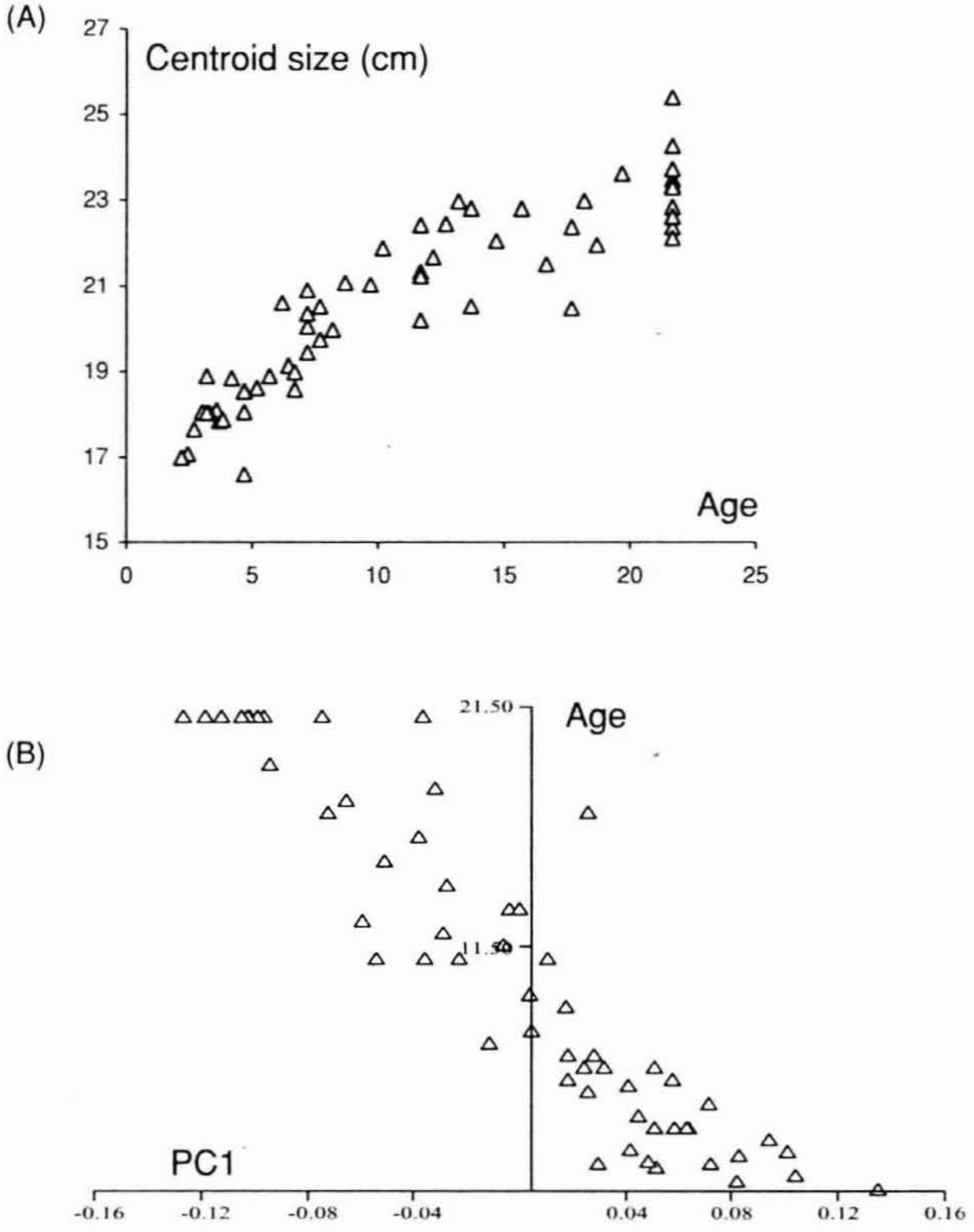


Figure 5.4 Caucasians: (A) Biological age vs. centroid size; (B) biological age vs. PC1; (C) centroid size vs. PC1.

rate. In turn, this finding predicts that the effect on form of facial modeling and remodeling remains more or less constant in anatomical location and rate throughout much, if not all, of the postnatal period. This finding concurs with that reported for the postnatal period up to eruption of the last permanent maxillary molar in *Cercocebus torquatus* (O'Higgins & Jones, 1998). However, in many remodeling studies (e.g., Kurihara *et al.*, 1980) there are subtle variations

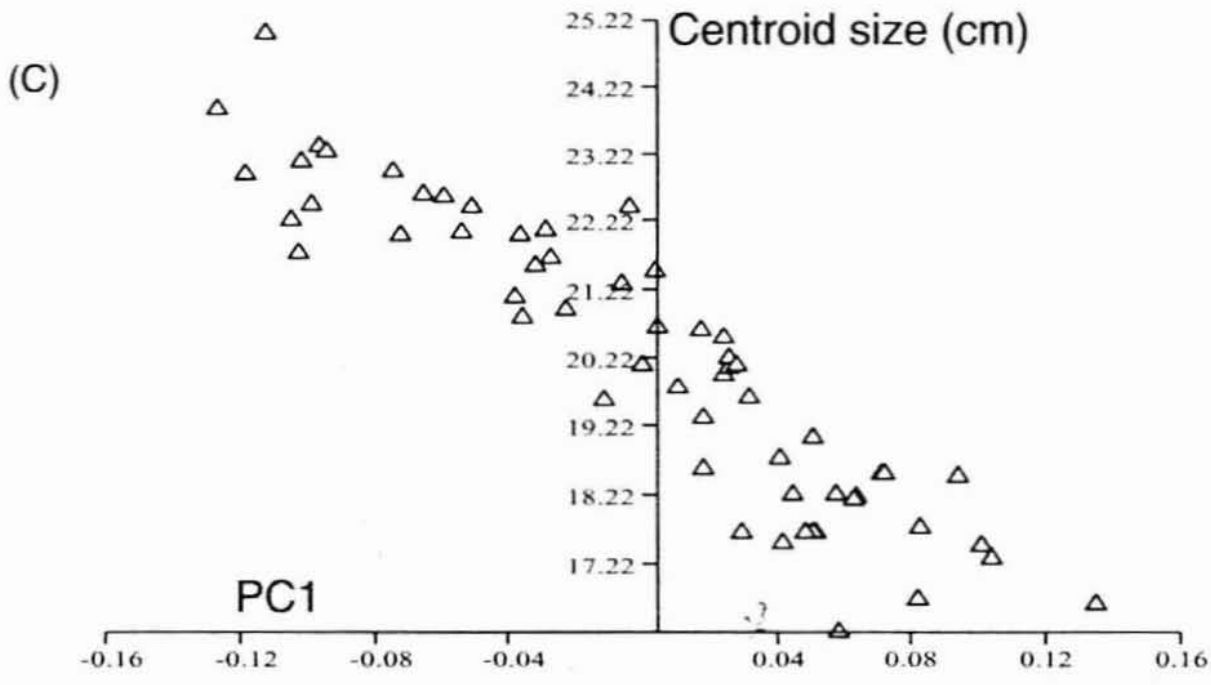


Figure 5.4 (*cont.*).

observed in the nature and location of remodeling fields during ontogeny. The findings of this study therefore indicate that these perturbations of remodeling must make only a small contribution to the ontogeny of facial form, at least of insufficient magnitude to present a detectable signal in cross-sectional studies of populations such as the present one. It will therefore be of interest to examine ontogeny within populations using longitudinal data in future studies.

Within the Arikara, the differences in facial shape between the small (Figure 5.2A and 5.2B) and large (Figure 5.2C and 5.2D) individuals include a relative reduction in the length of the frontal (Figure 5.2, label 1), a relative increase in maxillary height (Figure 5.2, label 2), a decrease in relative orbit size (Figure 5.2, label 3), a relative expansion of the zygomatic (Figure 5.2, label 4), a relative reduction in frontal breadth (Figure 5.2, label 5), relatively more superoposterior positioning of stephanion (Figure 5.2, label 6) representing the temporal muscle attachment, and an increase in relative alveolar prognathism (Figure 5.2, label 7). Are these features of ontogenetic shape change common to all the groups?

The answer from the analyses of ontogenetic shape trajectories is that some modern human populations grow along trajectories that are significantly different from one another. The magnitude of these divergences in terms of the size of the angle is comparable to that documented between species of non-human primates (Cobb & O'Higgins, 2002; O'Higgins *et al.*, 2001). We should be careful, however in how we interpret the magnitude of the angle since the degree of divergence of shape vectors says nothing about the actual features of anatomy that come to differ. This information is readily gleaned by careful comparison of visualizations of ontogenetic shape changes (examples of which are given in

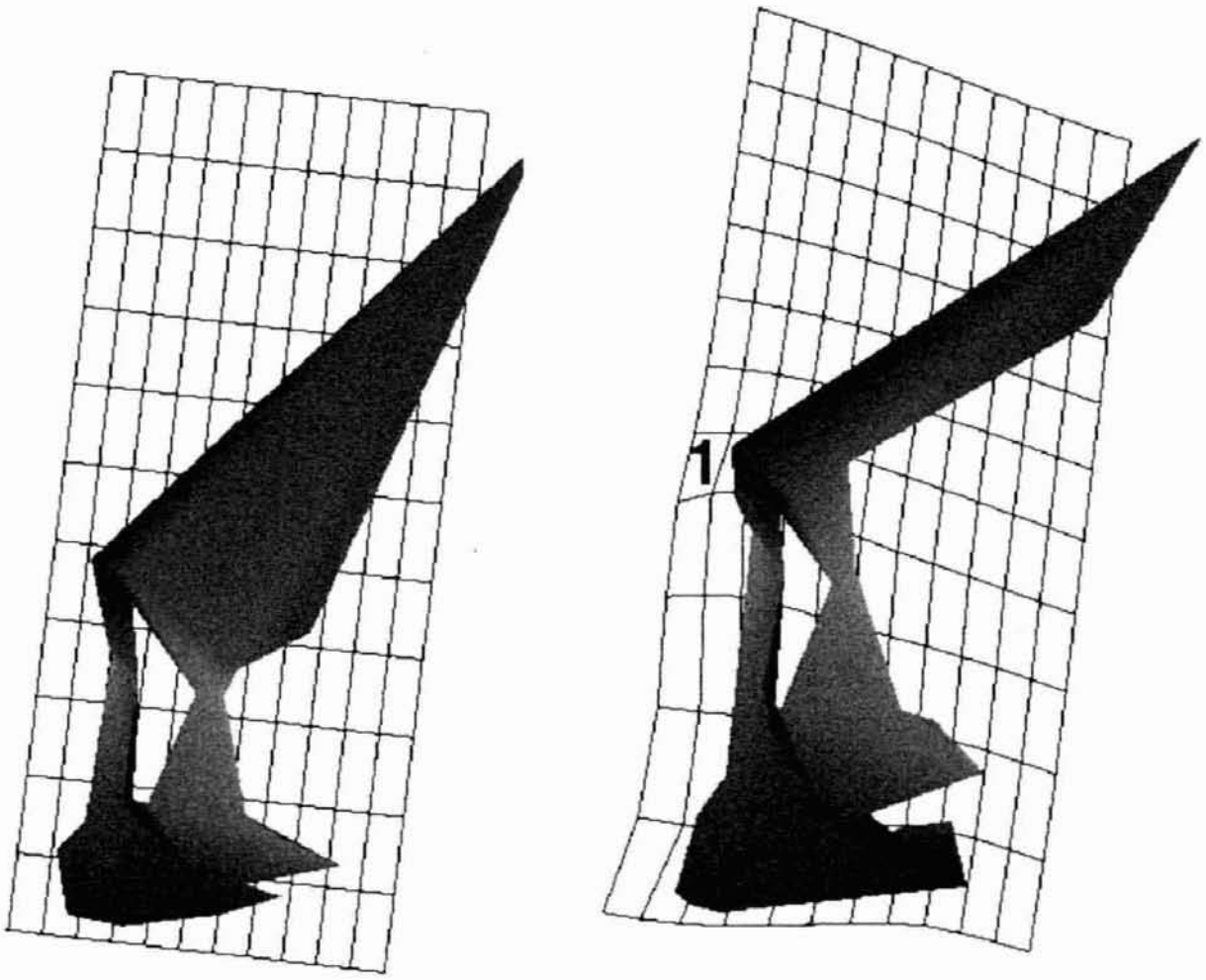


Figure 5.5 Caucasians: Morphological representations and transformation grids showing the variation in facial shape represented by PC1, from the positive (left, reference: PC1 0.14) to the negative extremes (right, target: PC1 −0.14), lateral view. See text for explanation of numbered label.

Figures 5.2 and 5.5). They show, for example, that unlike the other populations, Caucasians display a marked relative contraction of the supraorbital area with increasing size, which may be reflected in the statistically significant angle between the ontogenetic shape trajectory of the Caucasians and the other two populations. Although this study does not set out specifically to explore the underlying reasons for these observed differences in morphology, variations in supraorbital morphology have in the past been put down to differences in degree of neuroorbital disjunction (Hylander *et al.*, 1992; Ravosa, 1991; Weidenreich, 1941), or variation in supraorbital stress related to masticatory forces (see review of this issue by Leiberman, 2000). Although there is no consensus on this issue, the former is presently thought to be more likely, as bone in this region is often more robust than is needed to counter masticatory loads (Hylander *et al.*, 1992). Thus in the case of the Caucasians, it could be proposed that the divergence of their ontogenetic allometry from the other groups may, at least in part, be due to the development of a population-specific pattern of neuroorbital conjunction.

The fact that all the populations can be distinguished on the basis of facial shape, irrespective of the age of the individuals analyzed, is important in the context of the study of ontogeny in fossil hominins as well as for the sciences of archaeology and forensic anthropology. A larger study on a greater number of populations (Strand Viðarsdóttir *et al.*, 2002) has revealed that the relative relationships (calculated using Mahalanobis' distances) between the combined adult and subadult populations closely reflect those calculated from adults alone. This relationship illustrates that similar morphological features are likely to distinguish the adults and the subadults, although these may be accentuated and modified throughout ontogeny as a result of the divergence of the ontogenetic shape trajectories.

Overall, our findings illustrate the general plasticity of the modern human facial skeleton, and how our facial shape can be relatively easily adapted through minor shifts in the ontogenetic process. The population-specific morphologies documented here also imply that a great deal of caution should be called for in comparative morphological studies with subadults of other hominin species. Given the significant interpopulation differences in adult and subadult facial shape, studies of comparative development between modern humans and fossils that use "conglomerate" age series based on a number of populations (e.g., the recent example of Ponce de León & Zollikofer, 2001) may obscure the subtleties of possible growth similarities and differences in diverse human groups.

Our study indicates new possibilities for workers in paleoanthropology and paleontology as a whole. Once we have a greater understanding of ontogenetic variation within our own species, we may be in a better position to assess and evaluate possible levels of species distinction between other hominin subadults. The findings of this study also point to a tantalizing possibility with regard to the forensic identification of subadult skeletal remains. At present there is no way of reliably assigning subadult remains to ancestral groups on the basis of skeletal morphology. The cross-validation study of the full data set reveals that in the "classic" test case of differentiating Caucasians, African Americans, and Native Americans, the success of ancestry categorization is on par with that of form functions commonly used for adults (e.g., Giles & Elliot, 1962). It is our intention that these types of studies will eventually form the basis of an identification system for subadults similar to the adult based system of CRANID (Wright, 1992).

Conclusions

In this chapter we have discussed growth of the facial skeleton and demonstrated the large amount of variation that exists in the facial ontogeny of the one species

of the genus *Homo* that we can study comparatively. These results highlight the caution with which one should approach the study of ontogeny, but we hope that they have stimulated the reader's interest in the fascinating topic that is comparative ontogeny.

Acknowledgments

We thank Jennifer Thompson, Gail Krovitz, and Andrew Nelson for inviting us to participate in the symposium on "Growth in the Genus *Homo*" which formed the foundation for this book. We also thank the curators of the collections analyzed for access to the specimens in their care. Nick Jones deserves special thanks for his computing support, as do our colleagues in Durham and University College London for stimulating discussions. Chris Stringer deserves special thanks for his continued support of this work.

References

Bass, W. (1986). *Human Osteology: A Laboratory and Field Manual*. Columbia: Missouri Archaeological Society.

Batzer, M. A., Stoneking, M., Alegriahartman, M., Bazan, H., Kass, D. H., Shaikh, T. H., Novick, G. E., Ioannou, P. A., Scheer, W. D., Herrera, R. J., & Deininger, P. L. (1994). African origin of human-specific polymorphic Alu insertions. *Proceedings of the National Academy of Sciences of the USA*, **91**, 12288–12292.

Bookstein, F. L. (1989). Principal warps: Thin-plate splines and the decomposition of deformations. *Institute of Electrical and Electronics Engineers Transactions on Pattern Analysis and Machine Intelligence*, **11**, 567–585.

Bromage, T. (1986). A comparative scanning electron study of facial growth remodeling in early hominids. PhD dissertation, University of Toronto.

Brooks, S., & Suchey, J. (1990). Skeletal age determination based on the *os pubis*: A comparison of the Acsadi–Nemeskeri and Suchey–Brooks methods. *Human Evolution*, **5**, 227–238.

Brues, A. (1990). *People and Races*. Prospect Heights: Waveland Press.

Burrows, A. M., Richtsmeier, J. T., Mooney, M. P., Smith, T. D., Losken, H. W., & Siegel, M. I. (1999). Three-dimensional analysis of craniofacial form in a familial rabbit model of nonsyndromic coronal suture synostosis using Euclidean distance matrix analysis. *Cleft Palate Craniofacial Journal*, **36**, 196–206.

Canalis, E. (1993). Regulation of bone remodelling. In *Primer on Metabolic Bone Diseases and Disorders of Mineral Metabolisms*, ed. M. Favus, pp. 33–37. New York: Raven Press.

Cann, R. L., Stoneking, M., & Wilson, A. C. (1987). Mitochondrial DNA and human evolution. *Nature*, **325**, 31–36.

Cavalli-Sforza, L., Menozzi, P., & Piazza, A. (1994). *The History and Geography of Human Genes*. Princeton: Princeton University Press.

Cheverud, J. M., & Richtsmeier, J. T. (1986). Finite-element scaling applied to sexual dimorphism in rhesus macaque (*Macaca mulatta*) facial growth. *Systematic Zoology*, **35**, 381–399.

Cobb, S., & O'Higgins, P. (2002). The ontogeny of form variation in the African ape facial skeleton: A hierarchical approach to the interspecific comparison of ontogenetic trajectories. *American Journal of Physical Anthropology*, **34** (Suppl.), 55.

Collard, M., & O'Higgins, P. (2001). Ontogeny and homoplasy in the papionin monkey face. *Evolution and Development*, **3**, 322–331.

Corner, B. D., & Richtsmeier, J. T. (1991). Morphometric analysis of craniofacial growth in *Cebus apella*. *American Journal of Physical Anthropology*, **84**, 323–342.

Corner, B. D., & Richtsmeier, J. T. (1992). Cranial growth in the squirrel monkey (*Saimiri sciureus*): A quantitative analysis using three-dimensional coordinate data. *American Journal of Physical Anthropology*, **87**, 67–82.

Corner, B. D., & Richtsmeier, J. T. (1993). Cranial growth and growth dimorphism in *Ateles geoffroyi*. *American Journal of Physical Anthropology*, **92**, 371–394.

Djorovic, A., & Kalezic, M. L. (2000). Paedogenesis in European newts (*Triturus:* Salamandridae): Cranial morphology during ontogeny. *Journal of Morphology*, **243**, 127–139.

Dryden, I. L., & Mardia, K. V. (1992). Size and shape analysis of landmark data. *Biometrika*, **79**, 57–68.

Dryden, I. L., & Mardia, K. (1998). *Statistical Shape Analysis*. Chichester: John Wiley & Sons.

Eriksen, E., Vesterby, A., Kassen, M., Melsen, F., & Mosekilde, L. (1993). Bone remodeling and bone structure. In *Physiology and Pharmacology of Bone*, eds. G. Mundy & T. Martin, pp. 67–109. New York: Springer-Verlag.

Fehling, P., Alekel, L., Clasey, J., Rector, A., & Stillman, R. (1995). A comparison of bone mineral densities among female athletes in impact loading and active loading sports. *Bone*, **17**, 205–210.

Fink, W. L., & Zelditch, M. L. (1995). Phylogenetic analysis of ontogenetic shape transformations: A reassessment of the piranha genus *Pygocentrus* (Teleostei). *Systematic Biology*, **44**, 343–360.

Froment, A. (1992). Correspondence between anatomical differentiation and geographic distribution of modern humans studied by craniometry. *Comptes Rendus de l'Académie de Sciences de Paris*, **315**, 323–329.

Giles, E., & Elliot, O. (1962). Race identification from cranial measurements. *Journal of Forensic Science*, **7**, 147–157.

Gill, G., & Rhine, S. (eds.) (1990). *Skeletal Attribution of Race: Methods for Forensic Anthropology*, Anthropological Papers no. 4. Albuquerque: Maxwell Museum of Anthropology.

Good, P. (1993). *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses*. New York: Springer-Verlag.

Guglielmino-Matessi, C., Gluckman, P., & Cavalli-Sforza, L. (1977). Climate and the evolution of skull metrics in man. *American Journal of Physical Anthropology*, **50**, 549–564.

Hanihara, T. (1992). Population prehistory of East Asia and the Pacific as viewed from craniofacial morphology. *American Journal of Physical Anthropology*, **91**, 173–187.

Hanihara, T. (1996). Comparison of craniofacial features of major human groups. *American Journal of Physical Anthropology*, **99**, 389–412.

Heinonen, A., Oja, P., Kannus, P., Sievanen, H., Haapasalo, H., Manttari, A., & Vuori, I. (1995). Bone mineral density in female athletes representing sports with different loading characteristics of the skeleton. *Bone*, **17**, 197–203.

Hennessy, R., & Stringer, C. B. (2002). Geometric morphometric study of the regional variation of modern human craniofacial form. *American Journal of Physical Anthropology*, **117**, 37–48.

Hernandez, M., Fox, C. L., & Garcia Moro, C. (1997). Fueguian cranial morphology: The adaptation to a cold, harsh environment. *American Journal of Physical Anthropology*, **103**, 103–117.

Howells, W. W. (1973). *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of Difference among Recent Human Populations*. Cambridge: Harvard University Press.

Howells, W. W. (1986). Physical anthropology of the prehistoric Japanese. In *Windows on the Japanese Past: Studies in Archaeology and Prehistory*, eds. R. Pearson, G. Barnes, & K. Hutterer, pp. 85–99. Ann Arbor: Center for Japanese Studies, University of Michigan.

Howells, W. W. (1989). *Skull Shapes and the Map: Craniometric Analyses in the Dispersion of Modern* Homo. Cambridge: Harvard University Press.

Howells, W. W. (1995). *Who's Who in Skulls: Ethnic Identification of Crania from Measurements*. Cambridge: Harvard University Press.

Hunt, N. (1998). Muscle function and the control of facial form. In *Clinical Oral Science*, eds. M. Harris, M. Edgar, & S. Meghji, pp. 120–133. Oxford: Wright.

Hylander, W., Picq, P., & Johnson, K. (1992). Bone strain and the supraorbital region in primates. In *Bone Biodynamics in Orthodontic and Orthopaedic Treatment*, eds. D. Carlson & S. Goldstein, pp. 315–349. Ann Arbor: Center for Human Growth and Development.

Kendall, D. G. (1984). Shape manifolds, Procrustean metrics and complex projective spaces. *Bulletin of the London Mathematical Society*, **16**, 81–121.

Kurihara, S., Enlow, D., & Rangel, R. (1980). Remodeling reversals in anterior parts of the human mandible and maxilla. *Angle Orthodontics*, **50**, 98–106.

Lahr, M. M. (1995). Patterns of modern human diversification: Implications for Amerindian origins. *Yearbook of Physical Anthropology*, **38**, 163–198.

Lanyon, L. (1993). Skeletal responses to physical loading. In *Physiology and Pharmacology of Bone*, eds. G. Mundy & T. Martin, pp. 485–505. New York: Springer-Verlag.

Lanyon, L., & Rubin, C. (1984). Static versus dynamic loads as an influence on bone remodeling. *Journal of Biomechanics*, **17**, 892–905.

Leigh, S. R., & Cheverud, J. M. (1991). Sexual dimorphism in the baboon facial skeleton. *American Journal of Physical Anthropology*, **84**, 193–208.

Lieberman, D. E. (1996). How and why humans grow thin skulls: Experimental evidence for systemic cortical robusticity. *American Journal of Physical Anthropology*, **101**, 217–236.

Lieberman, D. E. (2000). Ontogeny, homology and phylogeny in the hominid craniofacial skeleton: The problem of the browridge. In *Development, Growth and*

Evolution: Implications for the Study of Hominid Skeletal Evolution, eds. P. O'Higgins & M. Cohn, pp. 85–112. London: Academic Press.

Lovejoy, C., Meindl, R., Mensforth, R., & Barton, T. (1985). Multifactoral determination of skeletal age at death: A method and blind test of its accuracy. *American Journal of Physical Anthropology*, **68**, 1–14.

Martin, R., Burr, D., & Sharkey, N. (1998). *Skeletal Tissue Mechanics*. New York: Springer-Verlag.

McLachlan, J. (1994). *Medical Embryology*. Wokingham: Addison-Wesley.

Meindl, R. & Lovejoy, C. (1985). Ectocranial suture closure: A revised method for the determination of skeletal age at death and blind tests of its accuracy. *American Journal of Physical Anthropology*, **68**, 57–66.

Monteiro, L. R., Cavalcanti, M. J., & Sommer, H. J. III (1997). Comparative ontogenetic shape changes in the skull of Caiman species (Crocodylia, Alligatoridae). *Journal of Morphology*, **231**, 53–62.

Moss, M. (1964). Vertical growth of the human face. *American Journal of Orthodontics*, **50**, 359–376.

Moss, M. (1968). The primacy of functional matrices on orofacial growth. *Dental Practice*, **19**, 65–73.

Moss, M. (1997a). The functional matrix hypothesis revisited. I: The role of mechanotransduction. *American Journal of Orthodontic and Dentofacial Orthopedics*, **112**, 8–11.

Moss, M. (1997b). The functional matrix hypothesis revisited. II: The role of an osseous connected cellular network. *American Journal of Orthodontic and Dentofacial Orthopedics*, **112**, 221–226.

Moss, M. (1997c). The functional matrix hypothesis revisited. III: The genomic thesis. *American Journal of Orthodontic and Dentofacial Orthopedics*, **112**, 338–342.

Moss, M. (1997d). The functional matrix hypothesis revisited. IV: The epigenetic antithesis and the resolving synthesis. *American Journal of Orthodontic and Dentofacial Orthopedics*, **112**, 410–417.

Moss, M., & Salentijn, L. (1969a). The primary role of functional matrices in facial growth. *American Journal of Orthodontics*, **55**, 566–577.

Moss, M., & Saletijn, L. (1969b). The capsular matrix. *American Journal of Orthodontics*, **56**, 474–490.

Nei, M., & Roychoudhury, A. K. (1993). Evolutionary relationships of human populations on a global scale. *Molecular Biology and Evolution*, **10**, 927–943.

Nur, N., & Hasson, O. (1984). Phenotypic plasticity and the handicap principle. *Journal of Theoretical Biology*, **110**, 275–297.

O'Higgins, P. (2000). The study of morphological variation in the hominid fossil record: Biology, landmarks, and geometry. *Journal of Anatomy*, **197**, 103–120.

O'Higgins, P., & Collard, M. (1999). Facial growth and sexual dimorphism in some papionin species. *American Journal of Physical Anthropology*, **28** (Suppl.), 214.

O'Higgins, P., & Collard, M. (2002). Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology*, **257**, 255–272.

O'Higgins, P., & Jones, N. (1998). Facial growth in *Cercocebus torquatus*: An application of three-dimensional geometric morphometric techniques to the study of morphological variation. *Journal of Anatomy*, **193** (P2), 251–272.

O'Higgins, P., & Strand Viðarsdóttir, U. (1999). New approaches to the quantitative analysis of craniofacial growth and variation. In *Human Growth in the Past: Studies from Bones and Teeth*, eds. R. Hoppa & C. Fitzgerald, pp. 128–160. Cambridge: Cambridge University Press.

O'Higgins, P., Chadfield, P., & Jones, N. (2001). Facial growth and the ontogeny of morphological variation within and between *Cebus apella* and *Cercocebus torquatus*. *Journal of Zoology*, **254**, 337–357.

Parfitt, A. M., Mathews, C. H. E., Villanueva, A. R., Kleerekoper, M., Frame, B., & Rao, D. S. (1983). Relationships between surface, volume, and thickness of iliac trabecular bone in aging and in osteoporosis: Implications for the microanatomic and cellular mechanisms of bone loss. *Journal of Clinical Investigation*, **72**, 1396–1409.

Ponce de León, M., & Zollikofer, C. (2001). Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature*, **412**, 534–538.

Ranly, D. (1980). *A Synopsis of Facial Growth*. Norwalk: Appleton & Lange.

Ravosa, M. J. (1991). The ontogeny of cranial sexual dimorphism in two Old-World monkeys – *Macaca fascicularis* (Cercopithecinae) and *Nasalis larvatus* (Colobinae). *International Journal of Primatology*, **12**, 403–426.

Reilly, S. M. (1990). Comparative ontogeny of cranial shape in salamanders using resistant-fit theta rho analysis. In *Proceedings of the Michigan Morphometrics Workshop*, eds. F. J. Rohlf & F. L. Bookstein, pp. 311–321. Ann Arbor: University of Michigan Museum of Zoology.

Relethford, J. H. (1994). Craniometric variation among modern human populations. *American Journal of Physical Anthropology*, **95**, 53–62.

Relethford, J. H., & Harpending, H. (1994). Craniometric variation, genetic theory, and modern human origins. *American Journal of Physical Anthropology*, **95**, 249–270.

Rhine, S. (1990). Non metric skull racing. In *Skeletal Attributions of Race: Methods for Forensic Anthropology*, Anthropological Papers no. 4, eds. G. Gill & S. Rhine, pp. 9–20. Albuquerque: Maxwell Museum of Anthropology.

Richtsmeier, J. T., Cheverud, J. M., Danahey, S. E., Corner, B. D., & Lele, S. (1993a). Sexual dimorphism of ontogeny in the crab-eating macaque (*Macaca fascicularis*). *Journal of Human Evolution*, **25**, 1–30.

Richtsmeier, J. T., Corner, B. D., Grausz, H. M., Cheverud, J. M., & Danahey, S. E. (1993b). The role of postnatal growth pattern in the production of facial morphology. *Systematic Biology*, **42**, 307–330.

Rohlf, F. J. (1998). On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Systematic Biology*, **47**, 147–158.

Rohlf, F. J. (1999). Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification*, **16**, 197–223.

Scheuer, L., & Black, S. (2000). *Developmental Juvenile Osteology*. London: Academic Press.

Schour, I., & Massler, M. (1941). The development of the human dentition. *Journal of the American Dental Association*, **28**, 1153–1160.

Shea, B. T. (1983). Allometry and heterochrony in the African apes. *American Journal of Physical Anthropology*, **62**, 275–289.

Shea, B. T. (1986). Ontogenetic approaches to sexual dimorphism in the anthropoids. *Human Evolution*, **1**, 97–110.

Slice, D. E., Bookstein, F. L., Marcus, L. F., & Rohlf, F. J. (1996). A glossary for geometric morphometrics. In *Advances in Morphometrics*, eds. L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor, & D. Slice, pp. 531–551. New York: Plenum Press.

Snow, C., Hartman, S., Giles, E., & Young, F. (1979). Sex and race determination of crania by calipers and computers: A test of the Giles and Elliot discriminant function in 52 forensic science cases. *Journal of Forensic Science*, **24**, 448–460.

Sokal, R., & Rohlf, F. J. (1995). *Biometry*. New York: W. H. Freeman.

Sperber, G. (1989). *Craniofacial Embryology*. Oxford: Wright.

Strand Viðarsdóttir, U. (1999). Changes in the form of the facial skeleton during growth: A comparative morphometric study of modern humans and Neanderthals. PhD dissertation, University College London.

Strand Viðarsdóttir, U., & O'Higgins, P. (2001). Geometric morphometrics and the analysis of variations in facial form: Robusticity of biological findings in relation to bilateral versus unilateral and missing landmarks. *Statistica*, **LXI**, 315–333.

Strand Viðarsdóttir, U.,O'Higgins, P., & Stringer, C. B. (2002). A geometric morphometric study of regional differences in the growth of the modern human facial skeleton. *Journal of Anatomy*, **201**, 211–229.

Stringer, C. B., Dean, M. C., & Humphrey, L. T. (1999). Regional variation in human mandibular morphology. *American Journal of Physical Anthropology*, **28** (Suppl.), 260.

Turner, C. I. (1992). The dental bridge between Australia and Asia: Following Macintosh into the East Asian heart of humanity. *Archaeology of Oceania*, **27**, 143–152.

Ubelaker, D. (1989). *Human Skeletal Remains: Excavation, Analysis, Interpretation*. Washington, DC: Smithsonian Institution Press.

Van Limborgh, J. (1970). A new view on the control of the morphogenesis of the skull. *Acta Morphologica Scandinavica*, **8**, 143.

Weidenreich, F. (1941). The brain and its role in the phylogenetic transformation of the human skull. *Transactions of the American Philosophical Society*, **31**, 321–442.

Wong, L., Dufresne, C. R., Richtsmeier, J. T., & Manson, P. N. (1991). The effect of rigid fixation on growth of the neurocranium. *Plastic and Reconstructive Surgery*, **88**, 395–403.

Wright, R. (1992). Correlation between cranial form and geography in *Homo sapiens*: CRANID – a computer program for forensic and other applications. *Archaeology of Oceania*, **27**, 105–112.